Landscape heterogeneity strengthens the relationship between β-diversity and ecosystem function

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Abstract

Consensus has emerged in the literature that increased biodiversity enhances the capacity of ecosystems to perform multiple functions. However, most biodiversity/ecosystem function studies focus on a single ecosystem, or on landscapes of homogenous ecosystems. Here we investigate how increased landscape-level environmental dissimilarity may affect the relationship between different metrics of diversity (α, β, or γ) and ecosystem function. We produced a suite of simulated landscapes, each of which contained four experimental outdoor aquatic mesocosms. Differences in temperature and nutrient conditions of the mesocosms allowed us to simulate landscapes containing a range of within-landscape environmental heterogeneities. We found that the variation in ecosystem functions was primarily controlled by environmental conditions, with diversity metrics accounting for a smaller (but significant) amount of variation in function. When landscapes were more homogeneous, α, β, and γ diversity was not associated with differences in primary production, and only γ was associated with changes in decomposition. In these homogeneous landscapes, differences in these two ecosystem functions were most strongly related to nutrient and temperature conditions in the ecosystems. However, as landscape-level environmental dissimilarity increased, the relationship between α, β, or γ and ecosystem functions strengthened, with β being a greater predictor of variation in decomposition at the highest levels of environmental dissimilarity than α or γ. We propose that when all ecosystems in a landscape have similar environmental conditions, species sorting is likely to generate a single community composition that is well suited to those environmental conditions, β is low, and the efficiency of diversity-ecosystem function couplings is similar across communities. Under this low β, the effect of abiotic conditions on ecosystem function will be most apparent. However, when environmental conditions vary among ecosystems, species

45 sorting pressures is different among ecosystems, producing different communities among
46 locations in a landscape. These conditions lead to stronger relationships between β and the
47 magnitude of ecosystem functions. Our results illustrate that abiotic conditions and the
48 homogeneity of communities influence ecosystem function expressed at the landscape-scale.

49

50 **Introduction**

51 Human activities have dramatic impacts on the abiotic conditions and biota of natural
52 ecosystems (Vitousek et al. 1997, Cardinale et al. 2012a). Atmospheric pollutants have affected
53 global temperatures (Forster et al. 2007), while a shift towards industrial-scale agriculture has
54 accelerated levels of nutrient release (Tilman 1999, Bouwman et al. 2009), leading to increased
55 rates of eutrophication (Dupas et al. 2015). The realized impacts of changes in temperature and
56 nutrient levels are not uniformly distributed across time and space, increasing heterogeneity in
57 abiotic conditions among ecosystems within a landscape and producing novel environmental
58 conditions (Ashcroft et al. 2009, Hobbs et al. 2009). Moreover, the dispersal of nutrient
59 pollutants within a landscape varies considerably depending on soil type, hydrology, land use
60 and topography (Heathwaite et al. 2005, Okubo and Levin 2013). Human activities may
61 therefore increase heterogeneity in temperature and nutrient conditions (hereon termed
62 "environmental dissimilarity") above levels generated by natural processes. These changes to
63 environmental conditions may directly alter rates of ecosystem functions (Gruber and Galloway
64 2008, Shurin et al. 2012), but also present critical challenges for understanding
65 biodiversity/ecosystem function relationships at the landscape scale.

66 Biodiversity varies among and within ecosystems on every spatial and temporal scale
67 (Barbour et al. 1999, Bailey et al. 2004, Resh 2007, Lefcheck et al. 2015), and its measure is

both scale- and question-dependent. Local diversity, the number of species occurring within a local ecosystem is usually referred to as α-diversity (hereon "α"). Landscape-level or regional diversity (i.e., the number of species observed across individual ecosystems) is termed γ-diversity (hereon γ). Turnover among communities within a region (differences in community composition or α among local ecosystems) has been broadly referred to as β-diversity (hereon "β", Whittaker 1972).

There is growing consensus among ecologists that higher biodiversity often begets increased levels of ecosystem functioning across many types of ecosystems (Cardinale et al. 2012a). In addition, the specific species present, particularly the functionally dominant species, can have major impacts on ecosystem function (Grime 1998, Naeem et al. 2012, Atwood et al. 2014a). However, with a few notable exceptions (Pasari et al. 2013, Barnes et al. 2016, Burley et al. 2016, Hautier et al. 2018, Winfree et al. 2018), the majority of empirical investigations of biodiversity-ecosystem function relationships have focused on local species richness (α). This focus on local species richness overlooks the scale dependence of the biodiversity-ecosystem function relationship (Isbell et al. 2017), and assumes that the processes driving the relationship are equal at the ecosystem and landscape level.

Within a single ecosystem, or a homogeneous landscape of abiotically similar ecosystems, species sorting may lead to a single, "functionally optimal" community, composed of taxa with a series of traits and population densities that are well suited to exploit available resources. Furthermore, theory suggests that community composition should be similar across such landscapes because the available niches ought to be filled by the same species in each ecosystem (Kraft et al. 2008). In this case, we would therefore expect that α would be similar among ecosystems, and both β and γ should be relatively low. In contrast, as environmental conditions

91 across landscapes differ, species sorting should result in local communities that differ in species
92 composition (Barnes et al. 2016). Each of these different communities then consists of species
93 best adapted to each local habitat (Winder et al. 2009), and potentially meaning that species
94 turnover (β) is more important to maintain ecosystem function than α at larger spatial scales
95 (Winfree et al. 2018). We therefore expect that as we move from the ecosystem scale to the
96 landscape scale, environmental heterogeneity within a landscape may mean there is no single,
97 functionally optimal community that is able to best perform ecosystem functions (Isbell et al.
98 2017, Winfree et al. 2018). In landscapes with a high degree of environmental heterogeneity, we
99 might observe similar levels of α if each ecosystem provides a similar amount of niche space, but
100 higher β and γ than in homogeneous landscapes. Moreover, higher levels of β may be associated
101 within increased ecosystem functioning in heterogeneous landscapes, as different communities
102 may perform different functions, and perform some functions to a greater degree, under different
103 environmental conditions (Thompson and Gonzalez 2016, Isbell et al. 2017). In addition,
104 changes to abiotic conditions may increase the importance of stochastic determinants of
105 community composition (Chase 2010), leading to changes in α, β, and γ and ecosystem functions
106 either directly (Burley et al. 2016) or indirectly (Barnes et al. 2016).

107 To understand how differences in landscape-level environmental dissimilarity can alter the
108 relationships among ecosystem functions and α β γ, we used data from an outdoor freshwater
109 mesocosm experiment in which invertebrate community composition and core ecosystem
110 functions were measured. Temperature and nutrient conditions were manipulated, and the
111 subsequent variation in conditions among mesocosms was used to create simulated landscapes
112 with differing levels of environmental dissimilarity. This approach allowed us to examine how
113 the relationships between ecosystem functions and α β γ varied with environmental dissimilarity.

For each mesocosm we measured two ecosystem functions that represent basal trophic resources in aquatic food webs: primary production and leaf litter decomposition. We predicted that much of the variation in these ecosystem functions would be controlled by nutrient and temperature levels in the landscape due to the importance of bottom-up control, especially the role of nutrients in controlling primary production (Harpole et al. 2011). With respect to the role of diversity, we hypothesized that at low levels of environmental dissimilarity, α and γ would be more strongly associated with landscape-level ecosystem functions than β. In this case, the absolute diversity within both individual ecosystems and the landscape as whole would influence landscape-level ecosystem function, and a single functionally optimal community would occupy all habitats within the landscape. However, at higher levels of environmental dissimilarity, we hypothesized that β would be more strongly associated with landscape-level ecosystem functions than either α or γ. When environmental conditions among ecosystems in a landscape differ, each ecosystem within the landscape has the potential to have a different community that is well adapted to the particular abiotic conditions of that ecosystem.

Methods

Experimental set-up and data collection

Experimental ponds consisted of twenty, 1136 L Rubbermaid® cattle water tanks housed at the University of British Columbia's pond facility (Vancouver, Canada) and represented a subset of treatments from a broader experiment (Greig et al. 2012, Kratina et al. 2012). This broader experiment contained mesocosms where a top predator had been added, and we elected to exclude these treatments from the current analysis to focus on the effects of nutrients and

136 temperature. Nutrient and temperature conditions among the ponds were diretly manipulated in a
137 2 x 2 fully factorial design. Nutrient levels within each pond were designated as either ambient
138 or elevated, with elevated conditions being achieved through monthly additions of 264 μg of
139 nitrogen L^{-1} (as $NaNO_3$) and 27 μg of phosphorus L^{-1} (as KH_2PO_4). Temperature treatments were
140 designated as either ambient or elevated. Heating tanks with 300W Hagen® aquarium heaters
141 produced temperatures 3°C above ambient tank temperatures. Nutrient and warming treatments
142 were randomly assigned to the 20 ponds, to generate four experimental treatment combinations
143 of five replicates each.
144 At the start of the experiment, mesocosms were inoculated with phytoplankton,
145 zooplankton, macroinvertebrates and sediments from local sources. The experimental conditions
146 were maintained for 16 months, during which time the tanks were open to allow natural
147 colonization of macroinvertebrates and plankton from local sources. We assume that due to the
148 close spatial proximity of the mesocosms (1m between mesocosms) there were minimal
149 differences in dispersal rates. This lack of differential dispersal rates, together with the fact that
150 identical communities were initially inoculated, would mean that differences in diversity were
151 generated predominantly through species sorting under the different treatment conditions within
152 the mesocosm, and stochastic processes. After 12 months, abundance data on 25 benthic macro-
153 invertebrates and 16 zooplankton taxa were used to calculate α, β, and γ diversity of consumers.
154 Benthic macroinvertebrates were sampled with two 0.02m^2 cylinder pipe samples per tank along
155 with quantitative wall and water column sweeps, whereas zooplankton were collected in a 10L
156 depth-integrated water column samples (details in Shurin et al. 2012; Kratina et al. 2012). We
157 also collected data on two ecosystem functions: leaf litter decomposition and net ecosystem
158 productivity (NEP). Decomposition rates were calculated by fitting negative exponential decay

159 models to the mass of leaf matter (bigleaf maple, *Acer macrophyllum*) present in 10 mm mesh
160 Nitex® bags at 0 and 8 weeks (Benfield 2007, Greig et al. 2012). Net ecosystem productivity was
161 calculated as the difference in O_2 concentrations between dawn and dusk for each mesocosm
162 (Shurin et al. 2012). This metric of NEP therefore measures the difference between
163 photosynthesis and respiration of the whole community over the course of the daylight hours.
164
165 *Simulated landscapes*

166 The 20 experimental ponds were arranged in all possible combinations to construct 4845 unique
167 simulated landscapes. These simulated landscapes were generated by randomly selecting a
168 unique, random sample without replication of 4 of the 20 ponds (Pasari et al. 2013). As there was
169 no spatial component to the experiment, the ecosystems placed into each experimental landscape
170 were selected independently of their spatial location. Environmental heterogeneity within the
171 landscape was indexed using a 2 x 2 matrix of environmental conditions. Each experimental
172 pond within the landscape was classified according to its environmental conditions, i.e. whether
173 its nutrient levels were ambient [1] or elevated [2], and whether temperature was ambient [1] or
174 elevated [2]. The environmental dissimilarity index was then calculated as the Manhattan
175 distance between the ecosystems.

176 The number of potential ecosystem combinations that can produce landscapes with
177 different environmental dissimilarities is substantially different (e.g. there are 20 different
178 mesocosm combinations that produce landscapes with a dissimilarity of 0, but 2000
179 combinations produce a dissimilarity of 7). We thus resampled simulated landscapes within each
180 level of environmental dissimilarity 2000 times to balance the number of landscapes across
181 dissimilarity levels. The experimental design includes two levels of temperature and two levels

of nutrients. Although changes in the two factors are unlikely to be exactly biologically equivalent, both increased nutrients and increased temperature represent ecosystem-level stressors that may generate pools of tolerant species that differ from communities under ambient conditions. Note that environmental dissimilarity index values of 1, 2 and 5 are mathematically impossible with this design.

For each simulated landscape, we calculated landscape-level values of α, β, and γ. The total diversity (γ) was partitioned into α and β components by decomposing the Shannon entropy (Jost 2007, 2010). This method of partitioning means that α and β components are independent of each other and can then be converted into their numbers equivalents (or true diversity) by taking the exponential value of each metric (Jost 2007). As this method generates α and β diversities that are independent of each other (Jost 2007), they can be included as uncorrelated variables within the statistical analyses. In addition, the partitioning of Shannon entropy into α and β components means that the resulting values depend both on the number of species and the number of individuals of each species (i.e. both species richness and species evenness), making them less sensitive to the detection of rare species and under-sampling (Beck et al. 2013). All these processes were performed using the "entropart" package in R programming language (Marcon and Hérault 2015).

The relationships between environmental dissimilarity, diversity, and ecosystem functions

To quantify how environmental dissimilarity affected each of α, β, and γ, we regressed each diversity type against the environmental dissimilarity index. As previous experiments have demonstrated relationships between biodiversity and both temperature and nutrient levels (Worm et al. 2002, Wang et al. 2009), the number of mesocosms that had elevated nutrients or elevated

205 temperature were included as covariates. The environmental dissimilarity index is independent of
206 the number of elevated nutrient or temperature mesocosms as there are multiple ways to produce
207 different values of the index. However, landscapes with an environmental dissimilarity of 8
208 always contained two mesocosms with elevated nutrients and two with elevated temperature
209 crossed in a 2x2 manner, hence nutrient and temperature levels were completely redundant in
210 landscapes with environmental dissimilarities of 8. We therefore excluded temperature and
211 nutrient covariates from these regressions.

212 We further determined how two ecosystem functions (NEP and leaf litter decomposition)
213 were associated with α, β, and γ. As NEP was estimated as the difference between
214 photosynthesis (of both phytoplankton and periphyton) and respiration (of both the planktonic
215 and benthic communities), we used measures of α, β, and γ based on the benthic
216 macroinvertebrates and zooplankton taxa within each mesocosm. However, in the case of leaf
217 litter decomposition, we used measures of α, β, and γ based only on non-predatory benthic
218 macroinvertebrates because zooplankton do not consume benthic leaf litter (Shurin et al. 2012).
219 First, we analyzed a single "global" model for each ecosystem function, and tested for an
220 interaction between each metric of diversity and environmental dissimilarity. A significant
221 interaction would indicate the relationship between landscape level and ecosystem function
222 differs with the level of environmental dissimilarity. After we found a significant
223 β:environmental dissimilarity interaction, we separately analyzed the relationship between each
224 ecosystem function and α, β, and γ with data from each of the six landscapes with environmental
225 dissimilarities of 0, 3, 4, 6, 7, and 8. These six separate analyses each produced a slope of the
226 relationship between each ecosystem function and α, β, or γ. As we were running six different
227 regressions, we applied a Bonferroni correction (Weisstein 2004) to avoid inflating the chances

of type 1 errors. This Bonferroni correction meant that we used an alpha level of 0.008 to determine significant differences. In order to understand the relative importance of α, β, γ and elevate temperature and nutrients, the R^2 value for the linear models was decomposed among factors using "lmg" metric from the "calc.relimp" function within the relaimpo package (Grömping 2006) in R. This metric decomposes the total R^2 value into non-negative portions for each variable, that sum up to the total R^2 (Lindeman et al. 1980). As the order in which variables are added to a model can influence their relative importance, this metric takes the relative importance of each variable averaged over every order in which the variables can be added into the linear model (Lindeman et al. 1980, Johnson and LeBreton 2004, Grömping 2006).

Many previous analyses of the relationships between biodiversity and ecosystem functions have utilized biodiversity metrics based on species richness, rather than abundance-weight metrics (Loreau et al. 2001, Cardinale et al. 2006, Lefcheck et al. 2015). In order to make our results more comparable to previous studies, we repeated the whole analysis using species richness instead of abundance weighed metrics and present the results as a supplementary sections (*Supplementary materials*). However, as the use of abundance weighted metrics has the potential to increase the amount of information contained in diversity measures (Barwell et al. 2015), and may have a greater impact on ecosystem functions than richness (Winfree et al. 2015), we focus on the abundance-weighted measures in the main text.

Results

When α, β, and γ were measured in terms of their numbers equivalents (true diversity), landscape-level mean α did not have a significant relationship with either the environmental

dissimilarity index, but was reduced by 1.06 ± 1.04 (mean ± S.E., n=4845) for every elevated temperature mesocosm. Mean α also decreased by 1.01 ± 1.002 for every elevated nutrient mesocosm within the landscape ($F_{(1,4841)} = 71.43$, $P < 0.001$). Landscape level β increased with increasing environmental heterogeneity, being 1.04 ± 1.006 (mean ± s.e.) higher when the environmental dissimilarity index was 8 compared with 0 (linear regression, $F_{(1,4841)} = 161.22$, $P < 0.001$, Fig. 2). However, we observed a wide range of β across all levels of environmental dissimilarity, and there was substantial overlap of the ranges (Fig. 2). This high level of overlap in β is critical to the following analyses, as it allows us to compare the relationship between β and ecosystem functions across the different levels of environmental dissimilarity. In addition, β increased by 1.03 ± 1.0035 for each mesocosm containing elevated nutrients ($F_{(1,4841)} = 1108.43$, $P < 0.001$), and increased by 1.03 ± 1.003 for each mesocosm with elevated temperature ($F_{(1,4841)} = 8.42$, $P < 0.001$). Landscape-level γ increased with environmental dissimilarity ($F_{(1,4841)} = 99.21$, $P < 0.001$), increased by 1.015 ± 1.0025 for every elevated nutrient mesocosm ($F_{(1,4841)} = 248.38$, $P< 0.001$) and decreased by 1.011 ± 1.0023 for each elevated temperature mesocosm ($F_{(1,4841)} = 144.51$, $P < 0.001$).

To understand the relationships between ecosystem processes, diversity metrics and environmental conditions, we regressed both NEP and decomposition against α, β, γ, and the number of mesocosms containing elevated temperature and nutrient treatments. Our global analysis of landscape-level NEP revealed a significant interaction between environmental dissimilarity and β (multiple linear regression, $F_{(1,4835)} = 8.69$, $P = 0.003$). Specifically, the positive effect of β on NEP and the amount of variation explained by β increased as environmental dissimilarity increased (Fig. 2). NEP was associated with significant changes in α and γ ($P < 0.001$), although neither diversity metric significantly interacted with environmental

dissimilarity. NEP increased by 13.65% ± 1.88% for each mesocosm containing elevated nutrients ($F_{(1,4835)} = 74.91$, $P < 0.001$), and increased by 2.75% ± 0.63% for each elevated temperature mesocosm ($F_{(1,4835)} = 17.67$, $P < 0.001$). NEP significantly increased as mean α increased at all levels of environmental dissimilarity ≥ 3 (Fig. 2a). Across all levels of environmental dissimilarity, the proportional change in NEP associated with α varied from 0.030 when environmental dissimilarity was 3, to 0.044 when environmental dissimilarity was 8 (Fig. 2b). NEP was involved in a significant positive relationship with β at environmental dissimilarity levels ≥ 3 (Fig. 2a), and accounted for between 0.034 and 0.080 of the variation in NEP (Fig. 2b). The relationships between NEP and γ were positive when environmental dissimilarity was ≥ 3 (Fig. 2a). The proportion of variation in NEP associated with γ ranged between 0.037 and 0.060 (Fig. 2b). The relationship between NEP and nutrients was positive across all environmental dissimilarities where it could be assessed (level 8 could not be assessed) (Fig. 2a), and changes in the number of elevated nutrient mesocosms were associated with most of the proportional variation (0.41-0.53, Fig. 2b). The relationship between NEP and temperature was positive across all levels of environmental dissimilarity where it could be assessed (Fig. 2a), and temperature accounted for between 0.010 and 0.017 of the proportional variation (Fig. 2b).

The global analysis revealed that landscape-level leaf litter decomposition was significantly associated with an interaction between β and environmental dissimilarity ($F_{(1,4835)} = 32.12$, $P < 0.001$). The direction of this interaction indicated that the slope of the relationships between β and decomposition increased with increasing environmental dissimilarity. Decomposition rates varied with both α and γ (both $P < 0.001$), although neither one significantly interacted with environmental dissimilarity ($P = 0.79$ and $P = 0.23$ respectively). Decomposition rates also increased by 9.46% ± 0.43% for each elevated nutrient mesocosm ($F_{(1,4835)} = 21.95$, P

296 < 0.001), and increased by 13.02% ± 0.50% for each elevated temperature mesocosm in the
297 landscape ($F_{(1,4835)} = 26.20$, $P < 0.001$).

298 When landscapes with different environmental dissimilarity values were assessed
299 separately, there was a positive relationship between decomposition and landscape α when
300 environmental dissimilarity was 3, a positive relationship when environmental dissimilarity was
301 8, but no significant relationship when environmental dissimilarity was 0, or 4 - 7 (Fig. 3a). The
302 proportion of variation in decomposition explained by α was generally low (0.007 – 0.01 of the
303 total variation, Fig. 3b). Our data showed a positive relationship between decomposition and β at
304 all levels of environmental dissimilarity other than 0, and the slope coefficient of the relationship
305 between decomposition and β increased as the environmental dissimilarity index increased (Fig.
306 3a). The proportion of variation in decomposition explained by β ranged between 0.01 and 0.14
307 (Fig. 3b). Decomposition was positively associated with γ at all levels of environmental
308 dissimilarity (Fig. 3a), although the amount of variation accounted for by γ decreased with
309 increasing environmental dissimilarity from 0.27 to 0.06 (Fig. 3b). At levels of environmental
310 dissimilarity where they could be assessed (< 8), decomposition rates were higher in landscapes
311 with elevated nutrient and elevated temperature mesocosms (Fig. 3a). These environmental
312 conditions accounted for the majority of the variation in decomposition (up to 0.35 for
313 temperature at environmental dissimilarity =0), although the proporiton they accounted for
314 decreased (Fig. 3b).

315 Quantitatively similar relationships between environmental dissimilarity, diversity, and
316 ecosystem functions were found for the analysis based on species richness rather than
317 abundance-weighted metrics (*Supplementary materials*). However, when diversity measures
318 were calculated using abundance-weighted metrics, they tended to account for slightly more of

319 the variation in ecosystem function than when based on species richness. This increase in
320 variation is likely linked to the extra information included in abundance weighted metrics, and
321 may also be related to a pattern of decreasing species evenness with increasing environmental
322 dissimilarity (*Supplementary materials, Fig. S4*)

323

324 **Discussion**

325 We provide evidence that as landscape-level environmental heterogeneity increases, β increases,
326 which in turn is significantly associated with differences in landscape-level expressions of two
327 ecosystem functions. In addition, while primary production and decomposition were primarily
328 controlled by environmental conditions, at the highest levels of environmental dissimilarity, β
329 appeared to explain a greater proportion of the variation in decomposition than either α or γ. This
330 relatively large impact of β compared to α or γ suggests that in landscapes with a high level of
331 spatial heterogeneity, the turnover of species among ecosystems is a more important driver of
332 this basal ecosystem process than the actual composition of species. Relationships between
333 biodiversity and ecosystem function have been investigated across a wide variety of systems
334 (Tilman and Downing 1994, Bellwood et al. 2003, Girvan et al. 2005, Hattenschwiler et al. 2005,
335 Atwood et al. 2015), but the majority of these previous studies focus on how biodiversity and
336 community composition affects the processes within a specific ecosystem (Tilman and Downing
337 1994, Reich et al. 2005), or rates of flux to neighboring ecosystems (Atwood et al. 2014b).
338 Recent experiments show that α, β, and γ can alter landscape-level patterns of ecosystem
339 function (Pasari et al. 2013, Hautier et al. 2018, Winfree et al. 2018). Our results build on those
340 studies by showing that the importance of β as a driver of ecosystem functions may depend on
341 the level of environmental dissimilarity among ecosystems in a landscape.

342 Our results revealed that as landscape-level environmental dissimilarity increased,
343 landscape-level β also increased, but we observed no concurrent changes in α. This relationship
344 between environmental dissimilarity and β is consistent with ecological niche theory (species
345 sorting), which proposes that different species are better adapted to different conditions
346 (Vandermeer 1972, Chase and Leibold 2003), and aligns with recent findings from temperate
347 forest (Barnes et al. 2016) and pollination systems (Winfree et al. 2018). Recent theory has
348 shown that as environmental dissimilarity increases, increased β becomes increasingly important
349 for stabilizing ecological communities (Wang and Loreau 2014, 2016). The positive relationship
350 we observed between environmental dissimilarity and β may therefore mean than community
351 stability is being maintained by increased species turnover as conditions across the landscape
352 become increasingly heterogeneous. In addition β and γ increased as the number of elevated
353 nutrient mesocosms in the landscape increased, while α decreased. Many studies have reported a
354 unimodal, hump-shaped relationship between nutrient concentrations and biodiversity (Barnett
355 and Beisner 2007, Cardinale et al. 2012b). Our finding of decreased alpha diversity with
356 increased numbers of elevated nutrient landscapes suggest that nutrient levels in the experiment
357 pass the threshold at which nutrients increase taxon dominance and reduce species richness
358 (Nygaard and Ejrnæs 2009). The decrease in α associated with increased temperature suggest
359 that this abiotic factor may represent a stressor on the ecosystem, reducing the diversity present.
360 The increase in β associated with elevated nutrients and temperature suggests that as nutrients
361 and temperature increase, stochastic determinants of community composition such as priority
362 effects become stronger (Chase 2010), enhancing dissimilarity among ecosystems.

363 The positive relationships between NEP and α and β at environmental dissimilarity
364 greater than 0 would suggest that high primary production is providing a resource that can lead to

high consumer diversity (Tilman et al. 1982, Chase and Leibold 2002). In addition, the greatest driver of primary production within the experiment was the number of elevated nutrient mesocosms within a landscape. Previous continental scale studies have also demonstrated that the majority of variation in primary productivity is driven by abiotic conditions, with diversity contributing far less (Burley et al. 2016). The combination of the positive relationship between α and β and primary production, together with the high proportion of variation associated with elevated nutrients suggests that, in our system, primary production and the invertebrate consumer community it supports is strongly influenced by bottom-up processes.

Rates of leaf litter decomposition were not associated with either α or β when environmental dissimilarity was 0, influenced by γ, but primarily controlled by elevated temperature and nutrients. The positive effect of elevated temperature on decomposition rates likely stems from higher temperatures increasing rates of microbial metabolism (Geraldes et al. 2012, Follstad Shah et al. 2017). The positive effects of elevated nutrients on decomposition may have occurred through a priming effect, as increased primary producer biomass leads to the production of algal-based C exudates that can stimulate bacterial growth (Danger et al. 2016). Unlike primary production, which can be influenced by both consumption and algal growth, litter standing stocks can only be influenced by consumption as there was no leaf litter addition. This lack of an addition mechanism could potentially explain why diversity had a stronger general impact on decomposition than primary productivity, where elevated nutrients are likely to promote algal growth and counteract the effects of consumption.

Our study provides compelling evidence that β-diversity may increase ecosystem functions across heterogeneous landscapes. Previous investigations using mesocosms observed that increased β generally did not affect mean levels of ecosystem function in landscapes with

similar abiotic conditions, although it did substantially increase the variance in rates of functional processes (Pasari et al. 2013). This previous observation is consistent with our results in that we found no significant relationship between β and either decomposition or primary production when all ecosystems within a landscape had the same environmental conditions. However, increased environmental dissimilarity led to both increased β, and an increase in the strength of the relationship between β and ecosystem functions, to the extent that β was more strongly associated with ecosystem functions than either α or γ. The relatively high importance of β as environmental dissimilarity increases agrees with previous field experiments investigating the relationships between diversity and ecosystem functions (Isbell et al. 2017, Winfree et al. 2018). These previous investigations specifically note that as the spatial scale over which ecosystem functions are measured increases, environmental conditions are likely to become increasingly heterogeneous, meaning different species are better suited to performing different functions (Winfree et al. 2018). As anthropogenic stressors affect some ecosystems more than others (Ashcroft et al. 2009), and can homogenize communities (Mondy and Usseglio-Polatera 2014), understanding the relationships between diversity, environmental heterogeneity and ecosystem functions is crucial to estimating the wider impact of human alteration of landscapes.

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410 **Literature cited**

411 Ashcroft, M. B., L. a. Chisholm, and K. O. French. 2009. Climate change at the landscape scale:
412 predicting fine-grained spatial heterogeneity in warming and potential refugia for
413 vegetation. Global Change Biology 15:656–667.

414 Atwood, T. B., R. M. Connolly, E. G. Ritchie, C. E. Lovelock, M. R. Heithaus, G. C. Hays, J. W.
415 Fourqurean, and P. I. Macreadie. 2015. Predators help protect carbon stocks in blue carbon
416 ecosystems. Nature Climate Change 5:1038–1045.

417 Atwood, T. B., E. Hammill, and J. S. Richardson. 2014a. Trophic-level dependent effects on
418 CO2 emissions from experimental stream ecosystems. Global Change Biology:1–11.

419 Atwood, T. B., E. Hammill, D. S. Srivastava, and J. S. Richardson. 2014b. Competitive
420 displacement alters top-down effects on carbon dioxide concentrations in a freshwater
421 ecosystem. Oecologia 175:353–61.

422 Bailey, R. C., R. H. Norris, and T. B. Reynoldson. 2004. Bioassessment of freshwater
423 ecosystems. Springer.

424 Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment
425 protocols for use in streams and wadeable rivers. USEPA, Washington.

426 Barnes, A. D., P. Weigelt, M. Jochum, D. Ott, D. Hodapp, N. F. Haneda, and U. Brose. 2016.
427 Species richness and biomass explain spatial turnover in ecosystem functioning across
428 tropical and temperate ecosystems. Philosophical Transactions of the Royal Society B:
429 Biological Sciences 371:20150279.

430 Barnett, A., and B. E. Beisner. 2007. Zooplankton biodiversity and lake trophic state:
431 Explanations invoking resource abundance and distribution. Ecology 88:1675–1686.

Barwell, L. J., N. J. B. Isaac, and W. E. Kunin. 2015. Measuring β - diversity with species abundance data. Journal of Animal Ecology 84:1112–1122.

Beck, J., J. D. Holloway, and W. Schwanghart. 2013. Undersampling and the measurement of beta diversity. Methods in Ecology and Evolution 4:370–382.

Bellwood, D. R., A. S. Hoey, and J. H. Choat. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecology Letters 6:281–285.

Benfield, E. F. 2007. Decomposition of leaf material. Pages 711–720 *in* R. Hauer and G. Lamberti, editors. Methods in Stream Ecology. Burlington.

Bouwman, A. F., A. H. W. Beusen, and G. Billen. 2009. Human alteration of the global nitrogen and phosphorus soil balances for the period 1970-2050. Global Biogeochemical Cycles 23.

Burley, H. M., K. Mokany, S. Ferrier, S. W. Laffan, K. J. Williams, and T. D. Harwood. 2016. Primary productivity is weakly related to floristic alpha and beta diversity across Australia. Global Ecology and Biogeography 25:1294–1307.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A.Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012a. Biodiversity loss and its impact on humanity. Nature 489:326–326.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Cardinale, J., D. M. Bennett, E. Nelson, and K. Gross. 2012b. Does productivity drive diversity

454 or vice versa ? A test of the multivariate productivity-diversity hypothesis in streams.
455 Ecology 90:1227–1241.

456 Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more
457 productive environments. Science 328:1388–1391.

458 Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity
459 relationship. Nature 416:427–430.

460 Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary
461 approaches. University of Chicago Press, Chicago.

462 Danger, M., J. Cornut, E. Chauvet, P. Chavez, and A. Elger. 2016. Benthic algae stimulate leaf
463 litter decomposition in detritus-based headwater streams : a case of aquatic priming effect?
464 Ecology 94:1604–1613.

465 Dupas, R., M. Delmas, J.-M. Dorioz, J. Garnier, F. Moatar, and C. Gascuel-Odoux. 2015.
466 Assessing the impact of agricultural pressures on N and P loads and eutrophication risk.
467 Ecological Indicators 48:396–407.

468 Follstad Shah, J. J., J. S. Kominoski, M. Ardón, W. K. Dodds, M. O. Gessner, N. A. Griffiths, C.
469 P. Hawkins, S. L. Johnson, A. Lecerf, C. J. LeRoy, D. W. P. Manning, A. D. Rosemond, R.
470 L. Sinsabaugh, C. M. Swan, J. R. Webster, and L. H. Zeglin. 2017. Global synthesis of the
471 temperature sensitivity of leaf litter breakdown in streams and rivers. Global Change
472 Biology 23:3064–3075.

473 Forster, P., V. Ramaswamy, P. Artaxo, T. Berntsen, R. Betts, D. W. Fahey, J. Haywood, J. Lean,
474 D. C. Lowe, G. Myhre, and others. 2007. Changes in atmospheric constituents and in
475 radiative forcing. Chapter 2. Page Climate Change 2007. The Physical Science Basis.

476 Geraldes, P., C. Pascoal, and F. Cássio. 2012. Effects of increased temperature and aquatic
477 fungal diversity on litter decomposition. Fungal Ecology 5:734–740.

478 Girvan, M. S., C. D. Campbell, K. Killham, J. I. Prosser, and L. a. Glover. 2005. Bacterial
479 diversity promotes community stability and functional resilience after perturbation.
480 Environmental Microbiology 7:301–313.

481 Greig, H. S., P. Kratina, P. L. Thompson, W. J. Palen, J. S. Richardson, and J. B. Shurin. 2012.
482 Warming, eutrophication, and predator loss amplify subsidies between aquatic and
483 terrestrial ecosystems. Global Change Biology 18:504–514.

484 Grime, J. P. 1998. Benefits of plant diversity to ecosystems: Immediate, filter and founder
485 effects. Journal of Ecology 86:902–910.

486 Grömping, U. 2006. R package relaimpo: relative importance for linear regression. Journal Of
487 Statistical Software 17:139–147.

488 Gruber, N., and J. N. Galloway. 2008. An Earth-system perspective of the global nitrogen cycle.
489 Nature 451:293–296.

490 Harpole, W. S., J. T. Ngai, E. E. Cleland, E. W. Seabloom, E. T. Borer, M. E. S. Bracken, J. J.
491 Elser, D. S. Gruner, H. Hillebrand, J. B. Shurin, and J. E. Smith. 2011. Nutrient co-
492 limitation of primary producer communities. Ecology Letters 14:852–862.

493 Hattenschwiler, S., A. V Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition
494 interrestrial ecosystems. Annual review of ecology, evolution and systematics 36:191–218.

495 Hautier, Y., F. Isbell, E. T. Borer, E. W. Seabloom, W. S. Harpole, E. M. Lind, A. S.
496 MacDougall, C. J. Stevens, P. B. Adler, J. Alberti, J. D. Bakker, L. A. Brudvig, Y. M.
497 Buckley, M. Cadotte, M. C. Caldeira, E. J. Chaneton, C. Chu, P. Daleo, C. R. Dickman, J.

M. Dwyer, A. Eskelinen, P. A. Fay, J. Firn, N. Hagenah, H. Hillebrand, O. Iribarne, K. P. Kirkman, J. M. H. Knops, K. J. La Pierre, R. L. McCulley, J. W. Morgan, M. Pärtel, J. Pascual, J. N. Price, S. M. Prober, A. C. Risch, M. Sankaran, M. Schuetz, R. J. Standish, R. Virtanen, G. M. Wardle, L. Yahdjian, and A. Hector. 2018. Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. Nature Ecology & Evolution 2:50–56.

Heathwaite, a. L., P. F. Quinn, and C. J. M. Hewett. 2005. Modelling and managing critical source areas of diffuse pollution from agricultural land using flow connectivity simulation. Journal of Hydrology 304:446–461.

Hobbs, R. J., E. Higgs, and J. a. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution 24:599–605.

Isbell, F., A. Gonzalez, M. Loreau, J. Cowles, S. Díaz, A. Hector, G. M. MacE, D. A. Wardle, M. I. O'Connor, J. E. Duffy, L. A. Turnbull, P. L. Thompson, and A. Larigauderie. 2017. Linking the influence and dependence of people on biodiversity across scales. Nature 546:65–72.

Johnson, J. W., and J. M. LeBreton. 2004. History and use of relative importance indices in organizational research. Organizational Research Methods 7:238–257.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439.

Jost, L. 2010. Independence of alpha and beta diversity. Ecology 91:1969–1974.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. Science 322:580–582.

520 Kratina, P., H. S. Greig, P. L. Thompson, T. S. a Carvalho-Pereira, and J. B. Shurin. 2012.
521 Warming modifies trophic cascades and eutrophication in experimental freshwater
522 communities. Ecology 93:1421–1430.

523 Lefcheck, J. S., J. E. K. Byrnes, F. Isbell, L. Gamfeldt, J. N. Griffin, N. Eisenhauer, M. J. S.
524 Hensel, A. Hector, B. J. Cardinale, and J. E. Duffy. 2015. Biodiversity enhances ecosystem
525 multifunctionality across trophic levels and habitats. Nature Communications 6:1–7.

526 Lindeman, R. H., P. F. Merenda, and R. Z. Gold. 1980. Introduction to Bivariate and
527 Multivariate Analysis (London, Foresman and Co.).

528 Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A.
529 Huston, D. Raffaelli, and B. Schmid. 2001. Biodiversity and ecosystem functioning: current
530 knowledge and future challenges. Science 294:804–808.

531 Marcon, E., and B. Hérault. 2015. **entropart** : An *R* Package to Measure and Partition Diversity.
532 Journal of Statistical Software 67.

533 Mondy, C. P., and P. Usseglio-Polatera. 2014. Using fuzzy-coded traits to elucidate the non-
534 random role of anthropogenic stress in the functional homogenisation of invertebrate
535 assemblages. Freshwater Biology 59:584–600.

536 Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The Functions of Biological Diversity in an Age
537 of Extinction. Science 336:1401–1406.

538 Nygaard, B., and R. Ejrnæs. 2009. The impact of hydrology and nutrients on species composition
539 and richness: Evidence from a microcosm experiment. Wetlands 29:187–195.

540 Okubo, A., and S. A. Levin. 2013. Diffusion and ecological problems: modern perspectives.
541 Springer Science & Business Media.

542 Pasari, J. R., T. Levi, E. S. Zavaleta, and D. Tilman. 2013. Several scales of biodiversity affect
543 ecosystem multifunctionality. Proceedings of the National Academy of Sciences
544 110:10219–10222.

545 Reich, P. B., J. Oleksyn, J. Modrzynski, P. Mrozinski, S. E. Hobbie, D. M. Eissenstat, J.
546 Chorover, O. A. Chadwick, C. M. Hale, and M. G. Tjoelker. 2005. Linking litter calcium,
547 earthworms and soil properties: a common garden test with 14 tree species. ECOLOGY
548 LETTERS 8:811–818.

549 Resh, V. H. 2007. Multinational, Freshwater Biomonitoring Programs in the Developing World:
550 Lessons Learned from African and Southeast Asian River Surveys. Environmental
551 Management 39:737–748.

552 Shurin, J. B., J. L. Clasen, H. S. Greig, P. Kratina, and P. L. Thompson. 2012. Warming shifts
553 top-down and bottom-up control of pond food web structure and function. Philosophical
554 Transactions of the Royal Society B: Biological Sciences 367:3008–3017.

555 Thompson, P. L., and A. Gonzalez. 2016. Ecosystem multifunctionality in metacommunities.
556 Ecology 97:2867–2879.

557 Tilman, D. 1999. Global environmental impacts of agricultural expansion: the need for
558 sustainable and efficient practices. Proceedings of the National Academy of Sciences of the
559 United States of America 96:5995–6000.

560 Tilman, D., and J. A. Downing. 1994. Biodivesity and stability in grasslands. NATURE
561 367:363–365.

562 Tilman, D., S. S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology: The role of
563 limiting nutrients. Annual Review of Ecology and Systematics 13:349–372.

564 Vandermeer, J. 1972. Niche theory. Annual review of ecology and systematics 3:107–132.

565 Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human Domination of
566 Earth Ecosystems (Vol 277, Pg 494, 1997). Science 278:21.

567 Wang, S., and M. Loreau. 2014. Ecosystem stability in space: α, β and γ variability. Ecology
568 Letters 17:891–901.

569 Wang, S., and M. Loreau. 2016. Biodiversity and ecosystem stability across scales in
570 metacommunities. Ecology Letters 19:510–518.

571 Wang, Z., J. H. Brown, Z. Tang, and J. Fang. 2009. Temperature dependence, spatial scale, and
572 tree species diversity in eastern Asia and North America. Proceedings of the National
573 Academy of Sciences of the United States of America 106:13388–92.

574 Weisstein, E. W. 2004. Bonferroni correction. Wolfram Research, Inc.
575 http://mathworld.wolfram.com/BonferroniCorrection.html.

576 Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon:213–251.

577 Winder, M., J. E. Reuter, and S. G. Schladow. 2009. Lake warming favours small-sized
578 planktonic diatom species. Proceedings. Biological sciences / The Royal Society 276:427–
579 435.

580 Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of
581 common species, not species richness, drives delivery of a real-world ecosystem service.
582 Ecology Letters 18:626–635.

583 Winfree, R., J. R. Reilly, I. Bartomeus, D. P. Cariveau, N. M. Williams, and J. Gibbs. 2018.
584 Species turnover promotes the importance of bee diversity for crop pollination at regional
585 scales. Science 359:791–793.

586 Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control
587 of species diversity and ecosystem functioning. Nature 417:848–851.

588

589

590 **Figure legends**

591 **FIG. 1.** β-diversity (measured as effective numbers) increases with increased environmental
592 heterogeneity. Open circles **O** represent raw data, solid line indicates fit of a linear regression
593 model, dashed lines indicate standard errors estimates.

594

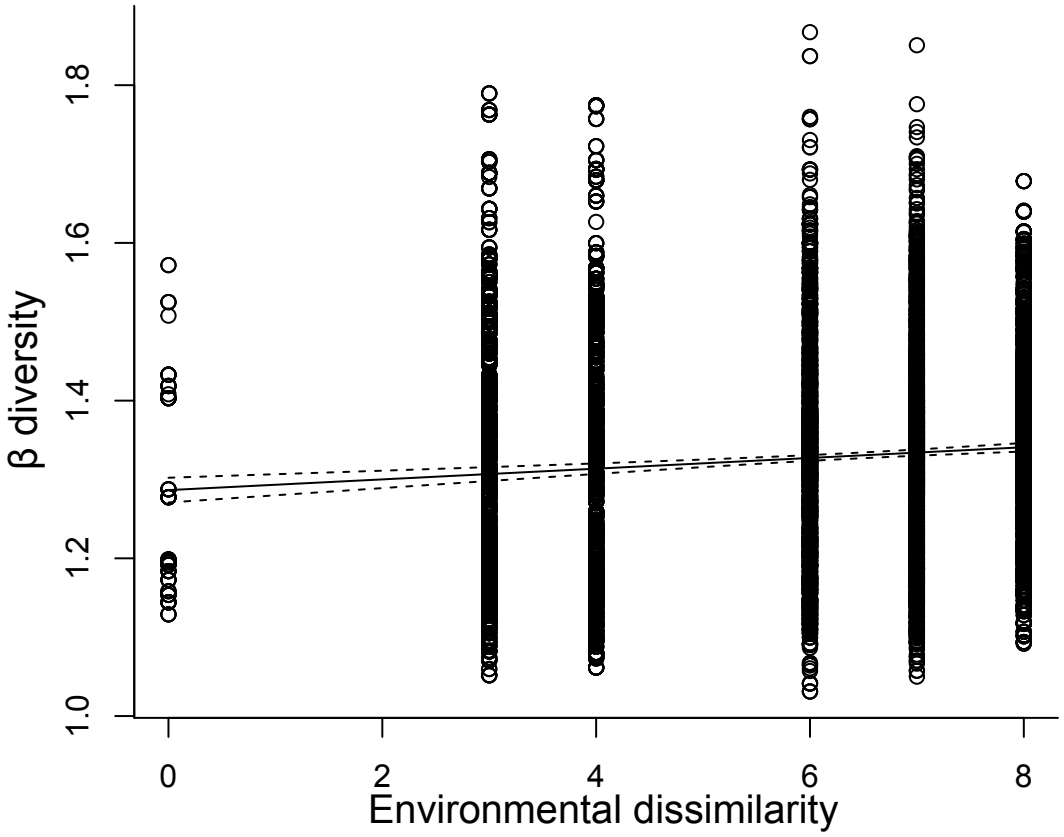
595 **FIG. 2.** Relationships between different metrics of biodiversity and environmental heterogeneity
596 on rates of net ecosystem production. A, slope coefficients for each factor taken from a linear
597 model incorporating all factors. B, proportion of the total variation in decomposition explained
598 by each factor. A star symbol (∗) indicates a relationship was not significant ($P > 0.008$
599 following a Bonferroni correction), an obelisk symbol (†) indicates there was no variation in a
600 factor, making a coefficient estimate impossible.

601

602 **FIG. 3.** Relationships between different metrics of biodiversity and environmental heterogeneity
603 on rates of leaf litter decomposition. A, slope coefficients for each factor taken from a linear
604 model incorporating all factors. B, proportion of the total variation in decomposition associated
605 with each factor. A star ("∗") indicates a relationship was not significant ($P > 0.008$ following a
606 Bonferroni correction), an obelisk ("†") indicates there was no variation in a factor making
607 obtaining a coefficient impossib

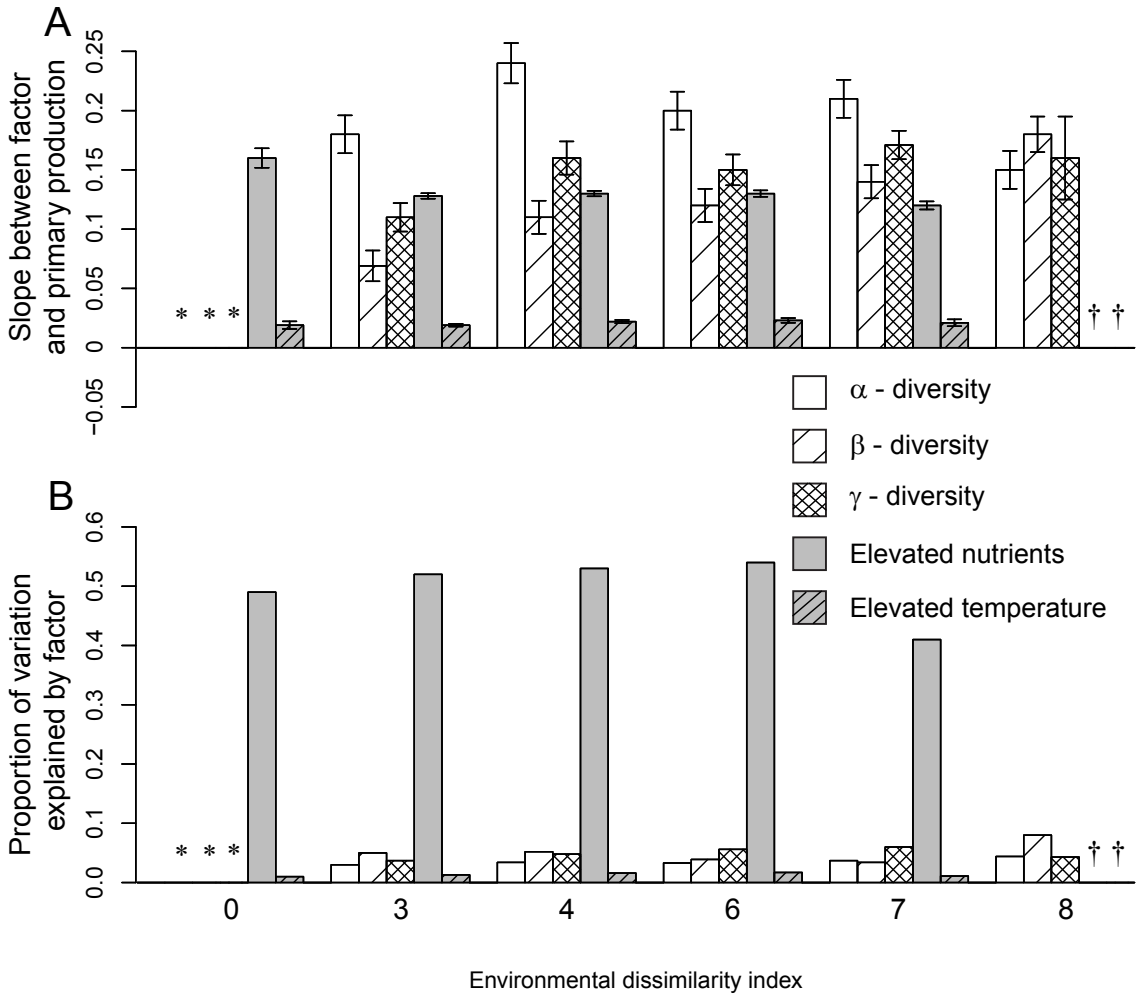
608

609


β diversity
1.0
1.2
1.4
1.6
1.8
0
2
4
6
8
Environmental dissimilarity

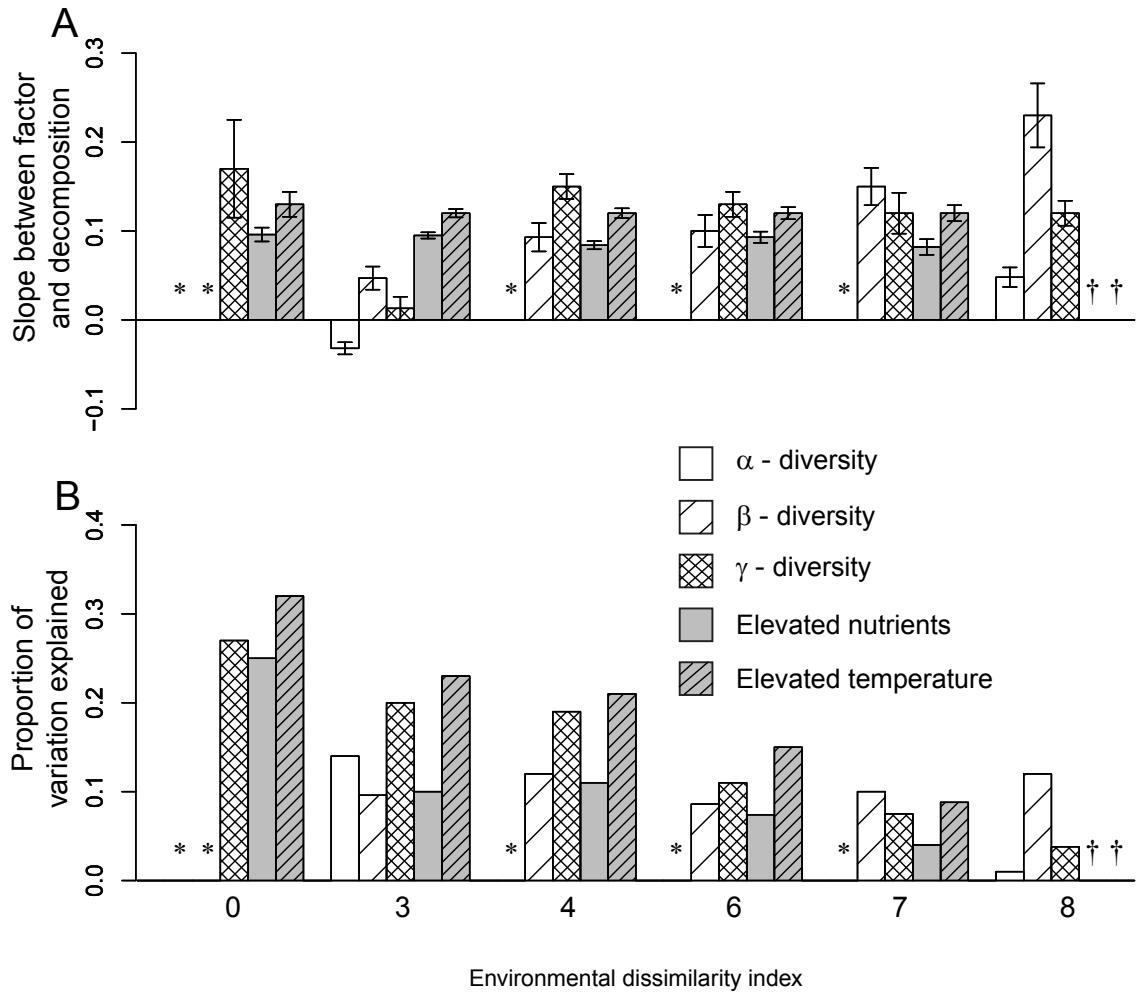
610

611 **FIG. 1.**


A
Slope between factor and primary production
0.25
0.2
0.15
0.1
0.05
0
−0.05
* * *
† †
α - diversity
β - diversity
γ - diversity
Elevated nutrients
Elevated temperature
B
Proportion of variation explained by factor
0.6
0.5
0.4
0.3
0.2
0.1
0.0
* * *
† †
0
3
4
6
7
8
Environmental dissimilarity index

612

613 **FIG. 2.**


A
Slope between factor and decomposition
0.3
0.2
0.1
0.0
−0.1
B
Proportion of variation explained
0.4
0.3
0.2
0.1
0.0
α - diversity
β - diversity
γ - diversity
Elevated nutrients
Elevated temperature
0
3
4
6
7
8
Environmental dissimilarity index

614

615 **FIG. 3.**